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THE MOVEMENT AND ACTIVITY PATTERNS OF SIMILAR-SIZED ADULT AND JUVENILE CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT. Adult male animals are commonly believed to exhibit higher activity than other conspecifics, but little information exists to compare their activity with that of other conspecifics of similar size. Here we compare the activity of adult male and similar-sized juvenile female crab spiders *Misumena vatia* (Araneae, Thomisidae). Adult males moved farther and more frequently than juvenile females of similar size (fourth instar) that were not affected by impending molt. Juvenile females influenced by impending or recent molt did not move as far or as frequently as nonmolting juveniles, even though their exoskeletons were hard enough to permit rapid movement. A small sample of penultimate males, of similar size to the adult males and juvenile females, exhibited activity patterns similar to the juvenile females. All of these data indicate that the high activity level of adult males is not a simple manifestation of behavior that is solely a function of size. We suggest that the high activity levels of the adult males facilitate search for scarce, cryptic mates.

Keywords: Activity level, molt, sit-and-wait predator

The high level of activity commonly attributed to reproductively active adult male animals is typically associated with searching for fertile females, a trait likely to enhance reproductive success by increasing contact with females (Thornhill & Alcock 1983; Andersson 1994). Seldom, however, is it explicitly established whether these perceived high activity levels of the males are unique to them.

Hypothetically, the size differences of juvenile and adult animals could by themselves account for their respective levels of activity. Adults of many species considerably exceed the size of younger individuals. However, one way to control the effect of size on activity is to compare the activity of different categories of a species that reach similar sizes (in this instance, adult males, juvenile females, and penultimate males). Size relationships such as the one considered here occur in species characterized by small adult males and large, relatively immobile adult females. In these systems, scramble competition for finding virgin females (Ghiselin 1974; Parker 2000) may result in high levels of activity by males, potentially driven by sexual selection.

The crab spider *Misumena vatia* (Clerck 1757) (Thomisidae) is an excellent species for addressing how activity rates vary over the life cycle. It is a sit-and-wait predator that hunts on flowers for visiting insect prey (Morse 1979; Morse & Fritz 1982). Males are tiny in relation to adult females, at times no more than 1% of the mass of gravid adult females (Gabritschevsky 1927; LeGrand & Morse 2000). Thus, they provide an opportunity to compare the activity of adult males with juvenile females of similar size. Although sit-and-wait predators, adult males have shorter giving-up times on hunting sites than adult females, penultimate females (both larger), or penultimate males (similar size) (Morse & Fritz 1982; Chien & Morse 1998; LeGrand & Morse 2000).

The difference in activity between adult females and adult males could be merely a consequence of the large adult females becoming less mobile than the earlier instars, or adult males becoming more active or both. Given the likely pressures of scramble competition, with adult male movement focused on finding virgin females (Vollrath & Parker 1992; Kotiaho et al. 1998), we predicted that adult

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males would move more rapidly (number of moves and distance per unit time) than other life-cycle stages. Since they often do not detect sexually mature females at distances exceeding 5 cm (Holdsworth & Morse 2000), male *M. vatia* should experience especially strong selection to move rapidly, thereby maximizing their number of visits to sites potentially occupied by these females (LeGrand & Morse 2000; Anderson & Morse 2001). Here we make the more critical comparison by testing the hypothesis that adult males are more active than other similar-sized conspecifics; i. e., fourth-instar females. We also test whether any such differences involve frequency of moves or length of moves. To obtain the appropriate data, we developed a practical method for quantitatively describing movement and activity levels of these spiders.

Like all arthropods, spiders spend most of their lives encased in jointed, chitinous exoskeletons, structures that provide protection and prevent desiccation. However, aside from their soft abdomen, spiders cannot increase in size except by molting, a state that profoundly affects activity and movement (Foelix 1996). Since *M. vatia* molt frequently (Gabritschevsky 1927), it was necessary to establish unequivocally whether the juveniles under study were influenced by impending molt, which could only be accomplished after establishing when an individual molted. It was thus also necessary to test the juveniles at both intermolt and molt periods, and we consequently present these results and comment upon them as well.

Voucher specimens of *Misumena vatia* have been deposited in the American Museum of Natural History.

METHODS

Study site and study organisms.—We conducted this study at the Darling Marine Center in South Bristol, Lincoln County, Maine. We performed all trials during June–August of 1998 and 1999 in a 3.5 ha field that is mown yearly in October.

Misumena vatia occur naturally at the study site and in surrounding fields and roadsides, spending most of their time in the herbaceous vegetation above 20 cm. They typically course through the fields, moving through most of the vegetation relatively quickly, but remaining on flowers, which they use for hunting sites, for considerably longer periods (Morse & Fritz 1982; LeGrand & Morse 2000). We used juvenile females comparable in size to the adult males. Other than being qualitatively sized by eye, they were randomly collected. We collected the *M. vatia* used in this study along roadsides adjacent to the study area. We recorded mass, carapace width, and length of leg 1 of each individual at capture. We also noted when a juvenile spider molted and took its new measurements. Except during measurements and behavioral trials, spiders were maintained individually in 7 dram clear plastic vials (5 cm tall, 3 cm diameter) and fed mosquitoes, flies and small moths every third day.

Movement and activity.—We observed both free-ranging spiders in the field and also monitored spiders in activity cages set in the field. Cages were 30 × 30 × 30 cm and covered on all sides, including the bottom, with dark green polyester mesh (8 × 10 mesh fibers/cm^2). We ran all trials in the field in clear weather during daytime hours, the time at which the majority of *M. vatia*'s activity occurs (Morse 1979; Morse & Fritz 1982).

In initial free-ranging trials we placed a focal spider on a stem of grass approximately 20 cm above the ground. To avoid sites that would slow spider movement, we ran all trials where no flowers were present, thus allowing us to record maximum searching capability, rather than movement confounded with extended visits to flowers. This measure should indicate the maximum distance the spiders would move over a unit of time and should also reflect their ability to locate a favored hunting site or object, be it a flower or a female. Following a 5 min acclimation period, free-range trials lasted 1 h, with activity and location recorded every 5 min, for a total of 12 observation times per individual. Depending upon the spider's position and activity at the instant of recording, five categories of activity were recognized: A). location changed since previous observation, in motion at moment observed (either traveling or changing orientation); B). location unchanged, but changing orientation at moment observed; C). location changed since last observation, but stationary; D). location unchanged, but orientation changed; E). neither location nor orientation changed, stationary. (Categories B, D and E cannot exclude the possibility that a spider has changed its location but then returned to it.)

We had originally intended to invest most of our efforts in measuring free-ranging individuals in the field. However, it quickly became apparent that we were losing so many individuals in the open field tests that it was extremely difficult to obtain complete runs of adult males before losing them. In particular, we frequently lost the small agile males in the vegetation and litter in spite of our best efforts to monitor them. Further, individuals lost prematurely usually moved more rapidly than those followed for an hour. Given the small sample available, it was not practical to run any of the penultimate males in the open field. The multiple runs needed to ascertain the molt stage of the juvenile females were also impractical because of the danger of losing them during one of these runs.

We thus gave up the efforts to measure free-ranging individuals in the field and concentrated on running cage trials. This technique provided a standardized substrate for measuring movement, thereby permitting direct comparison between individuals and between trials. The cages allowed us to eliminate hunting sites that would prevent accurate measurement of maximum activity levels. Most importantly, they eliminated the loss of male spiders. We used the same activity categories and times for individuals in the cage trials as for the field trials.

We positioned each cage in the open, directly on the ground, and transferred the spider from its vial to the middle of the mesh bottom of the cage. Positions of the spiders were determined with a millimeter rule, orientation noted, and changes measured and recorded at each 5 min interval. We thoroughly scrubbed the mesh and rotated the cages between runs to eliminate any possible position effects. Since exhaustive experiments have revealed no effect of pheromones on lines or in the air (Anderson & Morse 2001), we did not further control for this factor. We ran a maximum of four cage trials simultaneously, staggering the start by 1 min per cage.

Condition of nonmolting and molting individuals.—We divided the runs of the juvenile females into those affected by molts and those made at intermolt intervals. Molt periods encompassed the time when the integument commenced to break down, leading up to the molt, through the time when the integument of the next instar had completely hardened. Premolting changes can often be detected as parts of the integument begin to take on a somewhat transparent, vacuolated appearance, the start of the breakdown of the old integument. This change begins 4–5 d before molt (Foelix 1996); we therefore selected, a priori, the period from 5 d before molt to 1 d after molt as the "molting period", and the rest of the time as the "nonmolting period". Runs were performed independently of these periods, since we could only make the above-noted separation into nonmolting and molting condition after recording ecdysis. Tests on molting days were run only after the carapace had hardened enough so that the spiders were able to move about readily. All penultimate males had to be tested similarly to the females, and it was the failure of most of these individuals to remain in a nonmolting state over 5 d that resulted in the small sample size.

Analysis.—Each adult male and penultimate male contributed one activity trial to the analysis. Several juveniles contributed two trials, one as a "nonmolter" and one as a "molter". Juveniles were tested daily to determine when they could be incorporated into nonmolting and molting categories. Molting individuals were categorized as those between 5 d pre-ecdysis and one day post-ecdysis, following Foelix (1996). Only the first nonmolting run and first molting run were used for the analyses.

We obtained a measure of total activity for each individual: the number of 5 min periods in which an individual's activity warranted designation of Category A, B, C or D. A maximum performance would be 12, a score of 1 being assigned for each of the 5 min observation periods in which movement took place during an hour (Category A, B, C or D). We also calculated a high activity measure (number of Category A movements only) for the cage trials. We reasoned that individuals travelling at observation times likely moved more often than those whose positions changed, but were not observed in transit at observation times. We measured movement by summing the distances between an individual's locations on consecutively occupied sites. This measure gives a minimal possible distance traveled by the spiders; distances traversed during reversals of direction or roundabout

Table 1.—Total activity scores and distances (± SE) moved by free-ranging spiders.

Group	*n*	Activity score	Distance
Adult male	12	8.4 ± 0.58	197.9 ± 62.87
Juvenile female	10	7.0 ± 0.85	117.8 ± 25.46

circuits within a single observational period would not be recorded.

RESULTS

Mass and body dimensions.—Adult males (n = 32) weighed 5.2 ± 0.25 mg (x ± SE) when captured, with carapaces 1.4 ± 0.03 mm wide and legs 6.3 ± 0.13 mm long. Mass was positively correlated with carapace width (r = 0.690, $P < 0.001$, one-tailed product-moment correlation), and leg length (r = 0.373, $P <$ 0.05, same test). Carapace width and leg length were also positively correlated (r = 0.549, $P < 0.01$, same test). Sequential Bonferroni tests (Rice 1989) were applied to all of the correlations presented in this section.

The juveniles (n = 38) weighed 5.2 ± 0.40 mg and measured 1.3 ± 0.04 mm in carapace width and 4.9 ± 0.22 mm in leg length. Mass was positively correlated with carapace width (r = 0.743, $P < 0.001$, same test) and leg length (r = 0.713, $P < 0.001$, same test). Carapace width and leg length were positively correlated (r = 0.843, $P < 0.001$, same test). Males and females used in these experiments did not differ significantly in either mass (t = 0.090, $P > 0.9$) or carapace width (t = 0.287, $P > 0.5$), but did differ in limb length (t = 4.324, $P < 0.001$), all in two-tailed t-tests. Thus, males had longer legs than females of similar size.

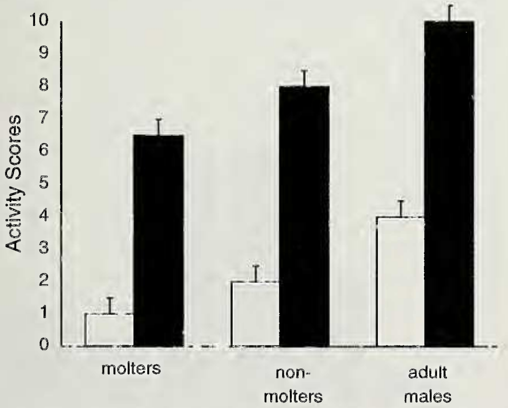

Figure 1.—Activity levels ± SD for adult males (n = 32), nonmolting juvenile females (n = 38), and molting juvenile females (n = 20). Black bars = total activity, white bars = high activity.

Free-ranging trials.—We present the data on free-ranging trials to illustrate the difficulty of obtaining velocity measures of adult males in the field and to justify our resort to the cage trials. In the free-ranging trials (Table 1), total activity scores of the adult males did not differ significantly from those of nonmolting juvenile females (U = 35.5, Z = 1.315, $P > 0.05$, one-tailed Mann-Whitney U-test). Neither did the distance traveled differ significantly between the two groups (U = 38, Z = 1.137, $P > 0.1$, same test). However, since both mean activity and mean total distance traveled by the adult males considerably exceeded those of the juvenile females (Table 1), the nonsignificant levels were likely a consequence of the especially high variance of the field individuals. Additionally, several rapidly moving males were lost in the field before adequate information could be gathered from them for a measurement. These results prompted our effort to design a method that would eliminate the losses of experimental subjects and that would decrease variance due to likely artifacts.

Cage trials.—Adult males were significantly more active (total activity scores) than nonmolting juvenile females (U = 394.5, n = 32, 38; Z = 2.517; $P < 0.02$, one-tailed Mann-Whitney U-test), and the difference in high activity scores between the two groups was particularly large (U = 229.5, Z = 4.462, $P < 0.0001$, same test) (Fig. 1). Adult males also moved greater distances than nonmolting juvenile females (U = 380, Z = 2.688, $P <$ 0.01, same test) (Fig. 2), a consequence of making both longer and more frequent moves (Figs. 1 & 2). We have not compared the contributions of these two variables statistically, because they are unlikely to be independent of each other.

Five penultimate males that fit the molting criteria (did not molt for 5 d following a run)

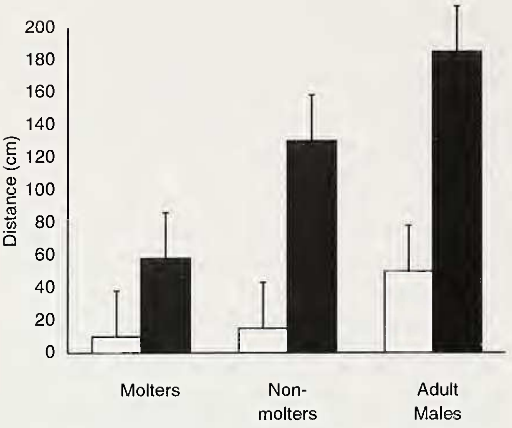

Figure 2.—Total distance moved (minimum/h) ± SD and mean lengths of single moves in cage trials by adult males, nonmolting juvenile females, and molting juvenile females. Black bars = total distance, white bars = mean length of single moves.

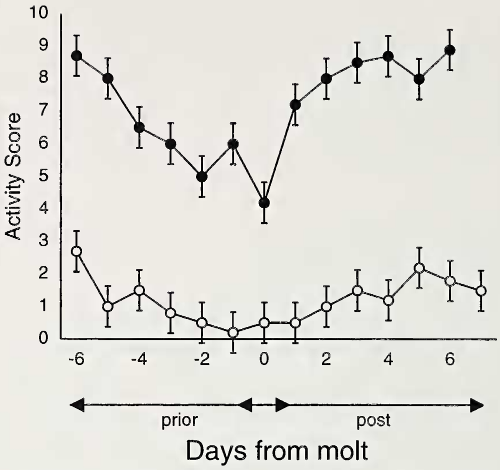

Figure 3.—Activity levels (total activity in black, high activity in white ± SD) of juveniles across a molting period. Days from molt depicted on horizontal axis such that 0 = molt day. Each point represents mean activity (± SD) of trials on molt day or specific number of days before or after molt.

exhibited activity levels similar to those of nonmolting juvenile females (total activity score = 6.3 ± 1.9; high activity score = 2.3 ± 1.0) ($U = 79$, $Z = 0.001$, $P > 0.9$; $U = 74.5$, $Z = 0.001$, $P > 0.9$ in two-tailed Mann-Whitney *U*-tests). We obtained no data on distance moved from these individuals. On the basis of these few individuals it thus does not appear that the adult male—juvenile female differences in activity we have reported are solely a consequence of the sex in question.

Activity near the molt.—In the process of establishing the molting state of juvenile females, we obtained considerable information about the activity levels of individuals in molting as well as nonmolting condition. These spiders exhibited a strong relationship between activity level and time before molt (Fig. 3). Both total activity and high activity scores dropped prior to molt, with a rapid return following ecdysis. The total activity score was lowest for individuals tested on their actual day of molt; the high activity score reached its minimum one day prior to molting (Fig. 3). None of the measurements included individuals with a nonfunctionally soft exoskeleton. Movements of individuals during molt and nonmolt periods differed significantly in total activity (Fig. 1: $T = 20$, $n = 20$, $Z = 3.546$, $P < 0.001$, one-tailed Wilcoxon matched pairs signed ranks test), high activity (Fig. 1: $T = 32$, $Z = 2.330$, $P < 0.02$, same test, and total distance traveled (Fig. 2: $T = 15$, $Z = 3.733$, $P < 0.001$, same test). This difference is a consequence of both the length and number of moves made by these individuals (Figs. 1 & 2).

The mean intermolt period was 20.6 ± 6.6 d (Fig. 4). Given a molt phase of approximately 6 d, a juvenile crab spider spent about one-third of its juvenile life in a molt phase, and about one-third of the juveniles were thus in a molt phase at any given time. The length of an instar did not correlate significantly with size (carapace width) ($T = 47$, $n = 14$, $Z = 0.345$, $P > 0.7$, two-tailed Wilcoxon matched pairs signed ranks test), nor did instar length

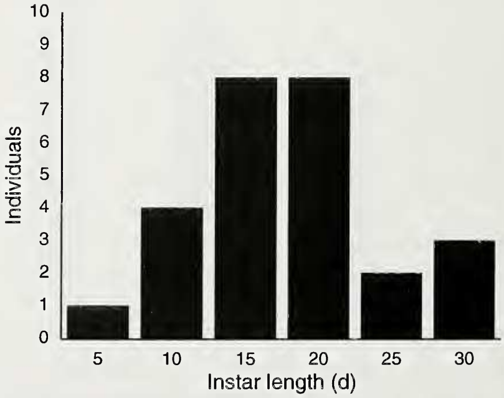

Figure 4.—Frequency distribution of time in days (d) between molts of juveniles.

correlate with the percentage of increase in size achieved via molt ($T = 43$, $n = 14$, $Z = 0.534$, $P > 0.5$, same test) or length of the preceding instar ($T = 19$, $n = 8$, $Z = 0.140$, $P > 0.8$, same test).

DISCUSSION

Animals with long, slender legs are often cursorial. Therefore, LeGrand & Morse (2000) hypothesized that, given the differences between juvenile females and penultimate males, the long legs of adult males facilitate rapid movement. In fact, the adult males in this study made significantly longer moves than did juvenile females. However, a substantial part of the difference between adult males and the other groups lay in the frequency of their moves, especially high-activity moves, rather than simply in the length of their moves. Thus, the difference in adult male movement cannot be attributed solely to differences in the shape of their legs.

Although one might argue that the cages provided an unnatural environment in which to run the experiments, the distances traveled by the spiders in the cages and in the open were similar (though less variable). The cages also exposed all of the spiders to the same conditions and cues. We therefore conclude that the cage trials served as an adequate estimate of movement rates of the different age and sex categories of these spiders in the field.

Innate behavioral factors might dictate the initiation of movements, as seen in the initiation of other behavioral patterns (Morse 2000) of *M. vatia*, but physiological mechanisms may dictate the length of the movements in part. Since spiders are physiologically severely limited in their ability to generate aerobic activity (Linzen & Gallowitz 1975; Anderson & Prestwich 1982), the adult males may avoid severe oxygen debts by restricting the lengths of their movements to the modest ranges observed, even though they exceeded those of the juvenile females. Even highly cursorial wolf spiders (Lycosidae) have tightly constrained sprint distances (Bristowe 1939; Morse 1997).

In other spiders investigated, females usually release pheromones prior to mating (e. g., Tietjen & Rovner 1982; Fernández-Montraveta & Ruano-Bellido 2000), behavior that attracts males, as a result of following lines "scented" with pheromones or, possibly, by airborne pheromones (Searcy et al. 1999). However, adult male *M. vatia* only detect females within a limited range of a few cm (LeGrand & Morse 2000) and follow draglines somewhat indiscriminately (Anderson & Morse 2001). Although the females are capable of mating immediately following molt (Holdsworth & Morse 2000), adult females in our populations on average were not mated until two to three days after molting, probably because, in the apparent absence of cues, the males could not locate them quickly (LeGrand & Morse 2000). The two-three day hiatus between molt and mating suggests that sizeable reproductive opportunities may be available to agile individuals. Therefore, males should be under extremely strong selective pressure to move frequently, quickly, and efficiently in order to find females. The high activity levels of the males should facilitate search for these cryptic females.

We initially planned extensive comparisons between adult males and penultimate males, which are of similar size, but penultimate males were available in the field for only limited periods in both the autumn and spring. We did not run them in the autumn out of concern that impending diapause might bias the results (Tauber et al. 1986; Tanaka 1992). In the spring most penultimate males molted within five days of their initial test and thus could not be used for this comparison, since before certifying a run for use in the analysis we had to establish that they were in a nonmolting state. The results from the small sample agree with the more general earlier findings of activity among penultimate males (LeGrand & Morse 2000) and strengthen the conclusion that the unique rates of adult male movement are not a mere consequence of sex, but are related directly to male maturation.

Juveniles 5 d prior to molt through 1 d after molt were significantly less active than nonmolting juveniles of the same size, whether using activity scores or distance traveled as criteria. Spiders tend to withdraw from sight and refuse prey for up to nearly a week prior to ecdysis (Foelix 1996). The initial decrease in activity of molting juveniles was probably a consequence of the onset of apolysis (separation of the new epidermis from the old cuticle). The commencement of apolysis is difficult to predict, but may precede ecdysis by up to a week in insects and spiders (Wigglesworth 1984; Foelix 1996). Differences in activity between molting and nonmolting juveniles resulted both from the molters moving less frequently and exhibiting far less high-activity behavior than nonmolting individuals. In contrast, the greatest difference between adult males and both molting and nonmolting females lay in the large amount of high-activity behavior in the adult males. Molting-condition juveniles thus exhibit severely constrained activity levels, which result in large part from a decline in the number of moves they make, rather than the length of moves. It must be emphasized that this low level of activity is not a consequence of a physical inability to move, since the period of forced inactivity resulting from a soft exoskeleton constitutes only several hours of the six-day period of low activity.

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